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Research Article

Odor increases synchronization of brain activity when watching emotional movies

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Abstract

Objective: Recent functional magnetic resonance imaging (fMRI) studies have shown that interpersonal synchronization of brain activity can be measured between people sharing similar emotional, narrative, or attentional states. There is evidence that odors can modulate the activity of brain regions involved in memory, emotion and social cognition, suggesting a link between shared olfactory experiences and synchronized brain activity in social contexts. **Method:** We used fMRI to investigate the effects of a positively-valenced odor on inter-subject correlation (ISC) of brain activity in healthy volunteers watching movies. While being inside an MRI scanner, participants ($N = 20$) watched short movie clips to induce either positive (happiness, tenderness) or negative (sadness, fear) emotions. Two movie clips were presented for each emotional category. Participants were scanned in two separate randomized sessions, once while watching the movie clips in the presence of an odor, and once without. **Results:** When all emotional categories were combined, the odor condition showed significantly higher ISC compared to the control condition in bilateral superior temporal gyri (STG), right middle temporal gyrus, left calcarine, and lingual gyrus. When splitting the movies according to valence, odor-induced increases in ISC were stronger for the negative movies. For the negative movies, ISC in the supramarginal gyrus and STG was larger in the second compared to first movie clips, indicating a time-by odor interaction. **Conclusion:** These findings show that odor increases ISC and that its effects depend on emotional valence. Our results further emphasize the critical role of the STG in odor-based social communication.

Keywords: Olfaction; social brain; intersubject correlation; fMRI; pseudo-hyperscanning; emotion

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Statement of Research Significance

Research Question

Odors can modulate the activity of brain regions involved in memory, emotion and social cognition, suggesting a link between shared olfactory experiences and synchronized brain activity in social contexts. Our main research question was whether exposure to a positive odor could enhance the synchronicity of brain activity in participants viewing emotional movie clips, using an fMRI pseudo-hyperscanning approach.

Main Finding

Watching emotional movie clips during odor exposure amplified synchronicity of brain activity among participants in superior and middle temporal gyri, and visual areas. The effect was dependent on the type of emotional content, with stronger effects for negative movie clips. The effects of odor for the negative movies increased over time, indicating a time-by odor interaction.

Study Contributions

These data offer a neurobiological perspective for the behavioral observations that odors may promote emotional contagion and enhance the similarity in how individuals perceive and experience the world.

Introduction

The ability to perceive, interpret, and engage in social interactions is a fundamental aspect of human behavior (Adolphs, 2009; Brothers, 1990; Frith, 2007). Trying to understand the behavior of others by attributing mental states to them helps us to recognizing and interpreting their beliefs, desires and emotions (Adolphs, 2009; Preckel et al., 2018), and is critical for living in a well-functioning social community. This social information can be conveyed through various means including eye gaze, body posture, facial expressions, voice tone, and body odors or fragrances (Ethofer et al., 2006; Gobel et al., 2015; Jack & Schyns, 2015; Li et al., 2023). These sensory cues

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are not just passive expressions but active conveyors of emotional states that facilitate emotional contagion (van Kleef & Cote, 2022). Consequently, this "contagion" through verbal and non-verbal cues, including odors, aligns emotion-related neural and physiological states among individuals, enhancing their ability to 'tune in' to each other, thus facilitating communication and mutual understanding (Herrando & Constantinides, 2021).

Odor perception plays an important role in social communication. For example, animals use smells to mark their territory, initiate sexual encounters, differentiate among individuals, and identify the emotional state of the other (Ache & Young, 2005; Ackerl et al., 2002; Doty, 1986; Ross & Martin, 2007). Studies have shown that natural body odors carry biological salience (Haegler et al., 2010; Iversen et al., 2015) and play a powerful role in creating a sense of connection between people (Calvi et al., 2020; Gomes & Semin, 2021; de Groot et al., 2012; de Groot et al., 2023). For example, odors can influence romantic relationships and partner selection through natural pheromones or shared fragrances [21]. Odors also contribute to parent-child bonding, as newborns can recognize their mother's scent (Kontaris et al., 2020; Soudry et al., 2011). Additionally, odors help create a distinct atmosphere in social settings, such as the use of incense in religious ceremonies or the aroma of food and drinks at social and family gatherings (Kontaris et al., 2020; Lee et al., 2022; Soudry et al., 2011).

The brain networks responsible for olfaction and emotion regulation substantially overlap (Kontaris et al., 2020). For instance, the amygdala, insula, anterior cingulate cortex, hippocampus, perirhinal cortex and orbitofrontal cortex respond to both emotional and olfactory cues (Soudry et al., 2011). Patients suffering from anosmia show gray matter reductions in emotion-related brain areas (Lee et al., 2022). There is also an important overlap between the olfactory and social brain networks. Regions critical to the social brain, such as the amygdala, medial prefrontal cortex, orbitofrontal cortex, insula, anterior cingulate cortex, temporal pole, and superior temporal gyrus (Prounis & Ophir, 2020), are also deeply involved in olfactory processing (Waymel et al., 2020).

Odors also influence areas associated with visual and auditory processing, subtly shaping social interactions (Boesveldt & Parma, 2021). The affective valence of the odor thereby plays an important role, with pleasant odors increasing and unpleasant odors decreasing social attraction (Cook et al., 2018; Demattè et al., 2007; Feng & Lei, 2022; Li et al., 2007). In this study we therefore focused on the effects of positive odors. Pleasantly scented odors enhance memory, attention, and mood regulation (Carlson et al., 2020), especially in social contexts, amplifying feelings of warmth and fostering positive interactions. Positive odors also modulate neural circuits by activating regions involved in social and emotional processing, such as the amygdala and orbitofrontal cortex (Watanabe et al., 2018; Winston et al., 2005). These odors enhance the perception of trust and warmth in social interactions and influence cognitive and motivational processes that persist beyond the initial olfactory input (Gaby & Zayas, 2017; Pause, 2012).

Recent functional magnetic resonance imaging (fMRI) studies indicate that engaging in shared social experiences, such as watching a film or listening to a story together, can lead to synchronized brain activity across individuals (Cohen and Parra, 2016; Hasson et al., 2004; Herbec et al., 2015; Mochalski et al., 2024; Nummenmaa et al., 2012; Nummenmaa et al., 2014; Smirnov et al., 2019; Speer et al., 2024). This synchronization may promote a deeper understanding of others and improve the ability to predict their thoughts, emotions, and actions (Cohen and Parra, 2016; Hasson et al., 2004; Mochalski et al., 2024; Nummenmaa et al., 2012; Nummenmaa et al., 2014; Smirnov et al., 2019; Speer et al., 2024). These studies have demonstrated that intersubject correlation (ISC) of brain activity across individuals exposed to the same stimulus, reflecting shared neural engagement, is influenced by factors such as the emotional content and complexity of the stimulus, shared background and experiences (i.e., friends vs. strangers), as well as individual personality traits and emotional or psychological states (Schore, 2021).

This study tested the hypothesis that adding a positive odor enhances ISC in brain regions linked to social perception in healthy participants watching emotional movie clips (Blomkvist & Hofer, 2021; Lubke et al., 2014; Spinella, 2002; Zou et al., 2016). More specifically, we predicted this effect to take place in brain areas implicated in synchronizing emotional states across individuals, including limbic areas (amygdala, anterior insula and thalamus) and areas involved in perspective-taking and social cognition (precuneus, temporoparietal junction and medial prefrontal cortex). This effect is expected due to the odor's ability to enhance emotional salience and multisensory integration, thereby strengthening shared neural responses and facilitating alignment in emotional and social processing.

Methods

Participants

Twenty healthy subjects (10 women, mean age: 34 ± 6.8 years; range: 22–45 years, Supplementary Table 1) took part in this study. All participants were right-handed, non-smoker, and had a normal sense of smell as assessed by the Sniffin Sticks test (Hummel et al., 2007). Individuals with a history of neurological disease or currently taking any medication affecting the central nervous system were excluded from participation. The research was completed in accordance with Helsinki Declaration and the study was approved by the ethics committee of the CHU UCL Saint-Luc (Brussels) (ethics approval number N°B403201112591). All participants provided written informed consent before taking part in the study.

Construction and validation of a video database

Based on a review of the available video databases designed to induce specific emotional states, we created a study-specific set of movie clips. After a comprehensive literature review (Gross & Levenson, 1995; Jenkins & Andrewes, 2012; Schaefer et al., 2010), we chose the French language-based database "FilmStim" (Supplementary Table 2) (Schaefer et al., 2010).This database includes 70 film sequences, lasting between 1 and 7 minutes, (Schaefer et al., 2010), from which we selected 30 sequences that we reduced to an average length of 95s (±10s). The clips were designed to induce two positive (amusement, tenderness) and two negative (fear, sadness) emotions in the viewers following a similar approach to that described by Nummenmaa et al., 2012. The shortened movie sequences were then tested in a panel of 16 participants (mixed men and women, aged between 18 and 45 years) to validate their effectiveness in inducing the intended emotional states.

Experimental design

We used a pseudo-hyperscanning approach, recording brain activity from individual subjects separately while they engage with the same task or stimulus, and then analyzing the data together as if they had been collected simultaneously. This is distinct from genuine hyperscanning, where multiple participants' brain activity is recorded simultaneously while they interact in real-time. Each

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participant completed two fMRI sessions, scheduled one week apart on the same day of the week and at the same time of the day (Mai et al., 2023; Merrow, 2023). Like in the study by Nummenmaa and co-workers (Nummenmaa et al., 2012), we presented the movie clips in a fixed order: amusement, fear, tenderness and sadness, totaling 21 minutes. The movie clips chosen are listed in Supplementary Table 2. The clips were displayed using an MRI-compatible screen positioned behind the magnet, reflected onto a mirror above the participant's eyes. Each movie was preceded by a short description (5 s) describing the context of the ensuring video clip without revealing its actual content (Nummenmaa et al., 2012). Each movie clip was followed by a blank screen with a central fixation cross. The order of the odor and control conditions was randomized across participants. In the odor condition, participants watched the movie clips while being exposed to lavender oil, belonging to the floral-woody olfactive space, dissolved in isopropyl myristate (an odorless and non-volatile solvent). The odor was administered by placing three drops on a cotton pad positioned on the head coil, 15–20 cm from the participant's nose inside the MRI room. In the control condition, participants watched a different series of movie clips of the same duration while exposed to an odorless agent, applied in the same manner. After the functional run, we acquired a 10-minute anatomical sequence (3DT1) for co-registration purposes.

Physiological and Behavioral measurements

Heart rate and respiration rate were measured during the fMRI data acquisition. Heart rate was measured using a pulse plethysmograph transducer, placed on the palmar surface of the left index finger. Respiration was measured using a respiratory effort transducer connected to an elastic respiratory belt encircling the chest. Both signals were subjected to a filtering process to remove potential artifacts. This process typically involves band-pass filtering within the range of 0.01 Hz to 0.1 Hz to eliminate high-frequency noise, baseline drifts, and motion artifacts, ensuring that only the essential physiological signals are retained for further analysis (Bancelin et al., 2023; Birn et al., 2006).

After the fMRI experiments, participants watched the same set of movie clips again on a laptop computer to rate in real time the valence and arousal (intensity of the perceived emotions) of each clip. Ratings were conducted offline because they might affect the neural responses during scanning (Hutcherson et al., 2005; Lieberman et al., 2007). Valence and arousal were rated on a scale ranging from 1 (negative valence/low intensity) to 10 (positive valence/high intensity). Valence and arousal were measured in separate runs.

Independent two-sample t-tests were used to compare the odor vs control conditions for each behavioral measure across different emotional states: amusement, tenderness, fear, and sadness. The null hypothesis assumed that there would be no difference between the odor and the control condition. A significance level (alpha) <0.05 was used for all statistical tests and corrections for multiple comparisons were applied.

MRI data acquisition

MR imaging was performed using a 3 T SIGNA™ Premier GE (General Electric, Milwaukee, US) with a 48-channel head coil at the CHU UCL Saint-Luc Hospital (Brussels). First, T2*-weighted echo-planar images were acquired with the following parameters: 2-mm slice thickness, TR = 1500 ms, TE = 30 ms, flip angle = 90 deg, FOV = 220 mm, voxel size 2x2x2 mm3, ascending interleaved acquisition. The fMRI run started with the presentation of a fixation cross (3s) in the center of the screen, followed by a "context" sentence (5s), and then the video sequence (90 ± 10s). The sequence concluded with participants completing a questionnaire related to the content of the video. The number of acquired volumes differed slightly between the odor (830 volumes) and control (816 volumes) conditions. Then, a T1-weighted structural image was acquired with a resolution of 1x1x1 mm^3.

MRI data pre-processing

The data were pre-processed using fMRIprep (Esteban et al., 2019). In order to correct for slice scan time, a sinc interpolation was performed using information regarding the repetition time (TR) (1500 ms) and the order of slice scanning, as specified in the original raw data. A three-dimensional head motion correction was conducted to address minor head movements by aligning all functional volumes of a subject with the initial volume through rigid body transformations. An examination of the estimated translation and rotation parameters indicated that they never exceeded 3 mm or 2°. The drift removal process entailed the elimination of linear trends and low-frequency nonlinear drifts with a periodicity of three cycles or fewer per time course, corresponding to a frequency of 0.0063 Hz. A Gaussian filter with a full width at half maximum of 5 mm was applied to the volume-based analysis following spatial interpolation to voxel space, in order to perform spatial smoothing. The functional data was aligned to the native anatomical data using a two-step procedure. Firstly, positional information derived from the header of the functional and anatomical scans was applied. Subsequently, a gradient-based alignment was employed to refine the alignment between the two datasets. The functional data were then normalized into a four-dimensional representation with a resolution of 2x2x2 mm, using the alignment information and the MNI "a12" transformation matrix obtained through the MNI normalization of the anatomical data.

fMRI analysis

The fMRI data were analyzed using BrainVoyager v.22.2.4 (Goebel et al., 2006; Goebel, 2012). The data analysis methodology focused on evaluating the temporal variations in the BOLD signal as participants watched video clips, drawing on the approach outlined by Nummenaa et al. (Nummenmaa et al., 2012). The process of ISC analysis starting with the calculation of voxel-wise temporal correlations among all participant pairs across the entire time series. Pairwise correlations were first computed between each subject's time-series data and that of every other subject. Within this approach the time series are divided into two segments for each of the four emotional categories (split 1 and split 2), resulting in eight segments in total. This procedure allows to test for the temporal dynamics over time within the same emotion category. For each emotion and condition, this step resulted in ((20*19)/2) 190 correlation pairs. Then, we averaged the ISC values within each subject, thus creating one value for each of the emotions and conditions. Finally, we used a Fisher z-transformation to overcome the limitations of the original r-value distribution (Bond & Richardson, 2004). The individual ISC maps were then employed in a second-level fMRI analysis to assess group-level synchrony and to identify statistically significant regions of ISC across the sample. To analyze the averaged and transformed ISC values at the second level, we applied a 2x2 Analysis of Variance with the factors "Odor" (levels: odor and control) and "Time point/Run" (levels: "split 1" and "split 2" for the first and second movie of each emotional category). This approach aimed to determine the main effects of each factor as well as their interaction, elucidating the

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differential impact of odor type and temporal dynamics on inter-subject neural synchrony.

In order to calculate the effect size of our study, we used the regression coefficient expressed as a function of the t-statistic (Serdar et al., 2021). For the post-hoc comparison of odor and control conditions, we achieved an r-value of 0.43, which qualifies as a medium (close to large) effect size.

Results

fMRI results

Main effect of emotional movies on ISC

Figure 1 displays the average ISC maps for the entire run, combining data from both the control and odor conditions. As shown, several large clusters of ISC were apparent, located in bilateral cuneus, occipito-parietal and occipito-temporal visual areas, bilateral superior and middle temporal gyrus and sulcus, bilateral parietal cortex, bilateral temporo-parietal junction, bilateral middle frontal, superior frontal and inferior frontal cortices, right precuneus and right posterior parietal cortex. No evidence for significant ISC was found in limbic brain areas. These findings are largely in line with previous research (Nummenmaa et al., 2012) and confirm that the selected movies in triggered synchronization of brain activity across participants (Figure 1, Table 1).

Main effect odor (full run)

The analysis of fMRI data revealed a significant main effect of odor condition when combining all emotions together (Figure 2, Table 2). Significantly stronger ISC during odor compared to the control condition was identified in bilateral STG, right middle temporal gyrus and left calcarine and left lingual gyrus.

Negative emotions

In a next step, we compared the effect of odor for the positive and negative movie clips separately. For the video clips with the negative emotions during the full run, there was a large cluster of increased ISC in the right calcarine area during odor stimulation (Figure 3, Table 3, upper part). Another large cluster was found in bilateral STG. Smaller clusters of increased ISC during the odor condition were found in superior occipital gyrus, cerebellum, left middle occipital gyrus (MOG) and visual areas right fusiform and lingual gyri (Figure 3, Table 3, upper part).

To investigate whether the effects of odor on ISC changed over time for a particular emotional condition, we applied a split run

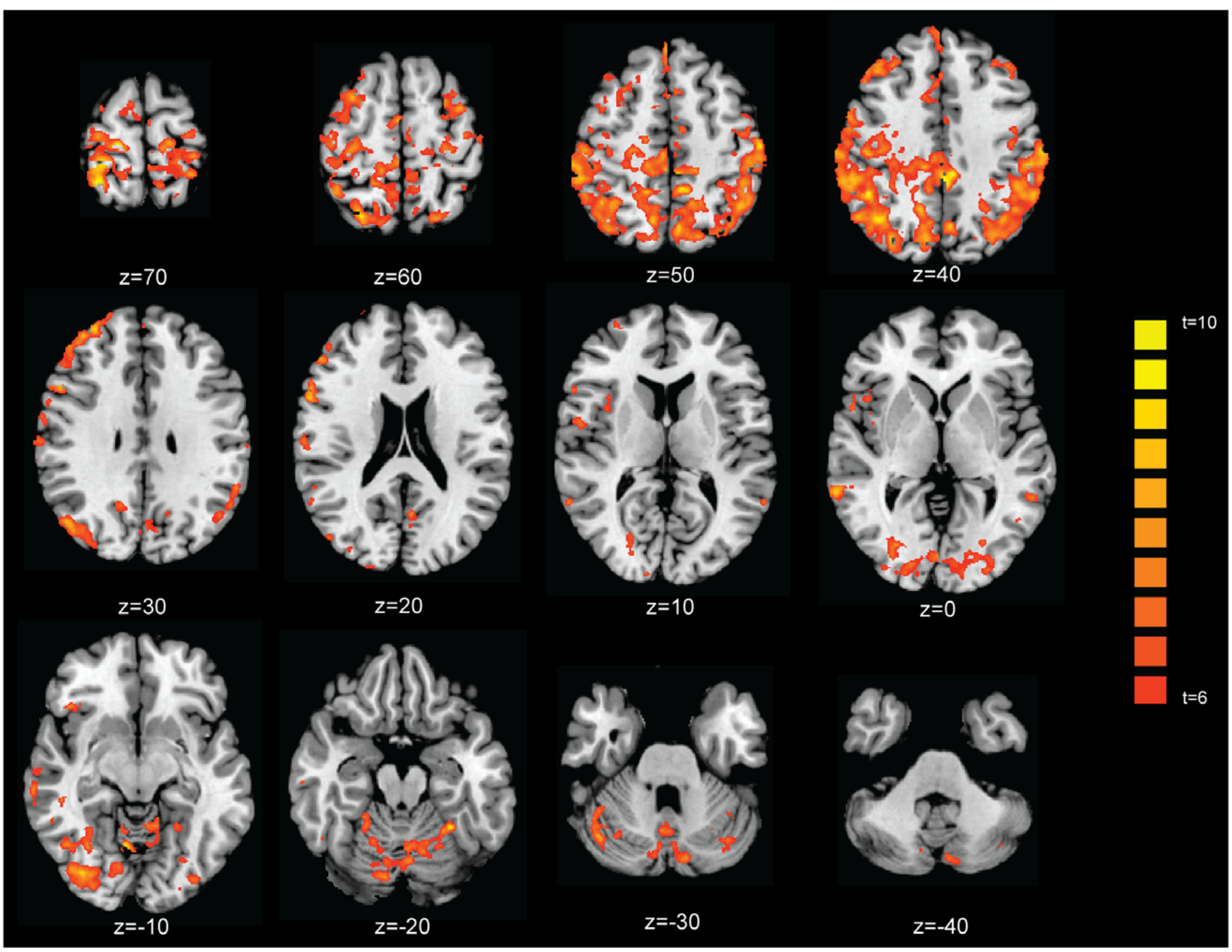

Figure 1. Brain areas showing statistically significant ($P < 0.05$, FDR-corrected) group-level ISCs during viewing of emotional movie clips (full run). Data show the results of the odor and control conditions combined. Right part of the images refers to the left side of the brain. Numbers below the slices refer to z-levels in MNI space. Several large clusters of ISC were found in the cuneus, precuneus, occipito-parietal and occipito-temporal visual areas, superior and middle temporal gyrus and sulcus, parietal cortex, temporo-parietal junction, middle frontal, superior and inferior frontal cortices, and cerebellum.

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Table 1. ISC during emotional videos (all emotions and conditions combined)

Brain structure	Size	Side	MNI Coordinates *x*	*y*	*z*	*t-stat*
Superior temporal gyrus	3344	R	63	−18	4	4,363
	1600	L	−63	−19	6	4,146
Middle occipital gyrus	1808	R	51	−71	8	6,843
	40	L	−32	−88	9	4,871
	432	L	−48	−73	10	4,217
Lingual gyrus	23,584	R	5	−86	2	6,202
Cuneus	200	R	28	−82	42	6,612
Parahippocampal gyrus	144	R	30	−51	−7	4,986
Inferior occipital gyrus	72	L	−45	−77	−4	5,782
Cerebellum	1200	R	31	−66	−52	4,525
	1648	R	19	−46	−48	5,009
	976	L	−14	−50	−50	4,948
Cingulate gyrus	832	R	9	8	42	5,734
Medial frontal gyrus	9168	L	−9	49	33	4,057

Abbreviations: R = right hemisphere; L = left hemisphere.

technique which allowed us to compare ISC during the first and second movie of each emotion type. For negatively-valenced movies, a large cluster of increased ISC was found in bilateral supramarginal gyrus (SMG), although stronger in the right hemisphere, when comparing the second with the first movie of the same emotional category. Additional ISC increases during the second movies were found in bilateral middle temporal gyrus, as well as in various brain areas involved in visual and auditory processing such as the left inferior temporal gyrus, left inferior occipital gyrus, left MOG, left STG, and left lingual gyrus (Figure 4, Table 3, lower part).

Positive emotions

For the positive movie clips, odor exposure increased ISC in the left angular gyrus, the left precuneus, left cuneus, left MOG and left STG (Table 4). Additional increases in ISC were observed in the cerebellum (including a smaller cluster in the right cerebellum Crus I and Crus II), inferior frontal gyrus, lingual gyrus, left precentral gyrus, bilateral precuneus, right posterior cingulate gyrus, and right superior frontal gyrus.

When comparing ISC of the first and second positive emotional clips (split-run) during odor exposure, significantly higher ISC was observed during the second movies in the left superior parietal gyrus, left inferior temporal gyrus, extending into the left lingual gyrus, left middle temporal gyrus, left inferior frontal operculum, right inferior temporal gyrus and right superior parietal gyrus (Table 4). These brain areas are related to sensory integration and emotional processing.

Behavioral results

Physiological results

Heart rate and respiration. Heart rate was not significantly different between the odor and control conditions during the presentation of amusement (t (38) = −0.55, P = 0.59, difference = 2.17 beats/minute) and fear movie clips (t (38) = −0.41, P = 0.68, difference = 1.61 beats/minute). Similarly, no significant differences were observed during the tenderness and sadness clips (Supplementary Figure 1). The respiration data also did not show a significant difference in the number of breaths per minute between the two conditions (Supplementary Figure 2).

Arousal and valence ratings. Participants rated valence and arousal on a scale from 1 (negative valence/low arousal) to 10 (positive valence/high arousal). Mean arousal ratings were 4.83 ± 3.24 (odor condition) and 4.38 ± 3.29 (control condition); (t (38) = −1.34, P = 0.19). Mean valence ratings were 4.47± ± 2.87 (odor condition) and 4.23 ± 2.64 (control condition; t (38) = −1.08, P = 0.28). (Supplementary Figure 3).

Discussion

The aim of this study was to test whether exposure to a pleasant odor affects intersubject synchronicity of brain activity. Participants

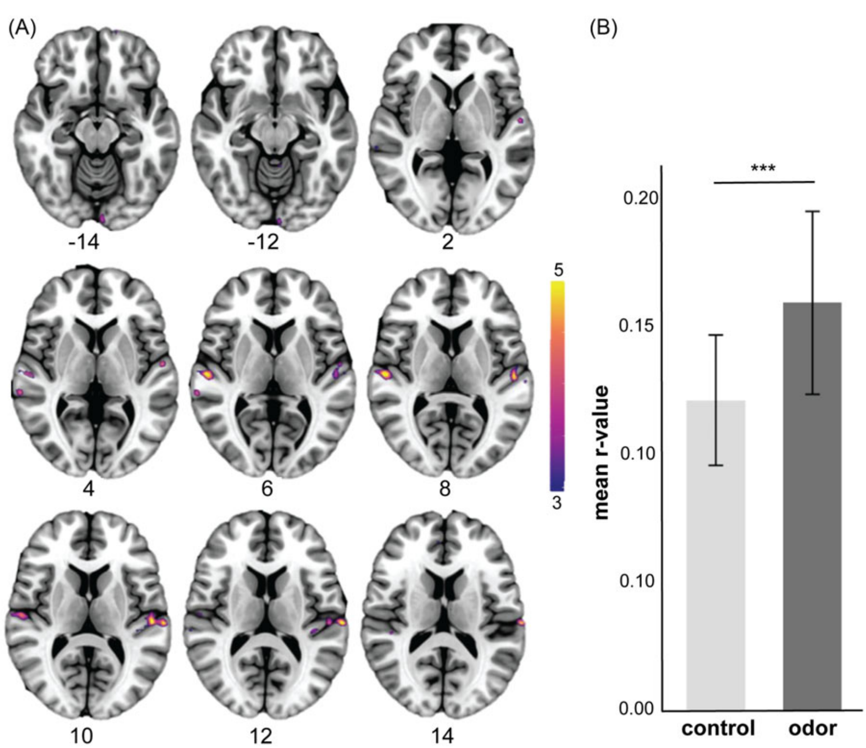

Figure 2. Main effect of the odor condition. **A.** Significant increases in ISC when comparing the odor with the odorless control condition ($P < 0.05$, FDR-corrected). Right part of the images refers to the left side of the brain. Numbers below the slices refer to z-levels in MNI space. Significantly stronger ISC was identified in bilateral STG, right middle temporal gyrus and left calcarine and left lingual gyrus in the odor compared to the odorless control condition. **B.** Average ISC values over all the significant voxels shown in A. The average correlation increased from $r = 0.116 \pm 0.06$ in the control condition to $r = 0.153 \pm 0.07$ in the odor condition ($t = 4.99$, $P < 0.01$).

Table 2. Increases in ISC when watching emotional movies during odor exposure (full run)

Brain structure	Size	Side	MNI Coordinates *x*	*y*	*z*	*t-stat*
Superior temporal gyrus	855	L	−66	−23	12	5.8
	550	R	58	−17	8	5.6
	46	L	−42	−29	12	3.7
Calcarine	140	L	−4	−91	−16	4.1
Middle temporal gyrus	104	R	66	−33	6	4.5

Abbreviations: R = right hemisphere; L = left hemisphere.

watched various types of emotional movie clips under tonic exposure of either a positively-valenced odor or an odorless control substance. Participants served as their own control. Our data confirm the hypothesis that adding a positive odor amplifies synchronicity of brain activity among participants watching similar emotional movies. When combining all emotional categories, the odor condition showed significantly higher ISC compared to the control condition in bilateral superior temporal gyri (STG), right middle temporal gyrus, left calcarine, and lingual gyrus. Emotional valence thereby played a significant role since the odor affected ISC more for the negative than the positive movie clips. Finally, we showed that the effects of odor increased over time, indicating a time-by odor interaction. These data offer a physiological perspective for the behavioral observations that odors may promote emotional contagion and enhance the similarity in how individuals perceive and experience the world.

At a general level, our data support previous findings that watching emotional movies increases ISC (Nummenmaa et al., 2012). Indeed, emotional movies augmented ISC in a number of cortical areas, including both primary and higher-order visual and auditory cortices, as well as parts of the brain social network (Cohen and Parra, 2016; Hasson et al., 2004; Hasson et al., 2012; Herbec et al., 2015; Nummenmaa et al., 2012), further supporting the claim that emotions promote interpersonal bonding. When adding an odor, ISC increased in temporal (bilateral STG and right middle temporal gyrus) and occipital (left calcarine and left lingual gyrus) brain areas. Earlier studies have highlighted the role of the STG and inferior occipital cortex in emotional and social brain processing. While the STG is typically associated with auditory and speech perception, it is also crucial for emotional processing, emotional learning, and conditioning (Cambiaghi et al., 2016; Concina et al., 2019; Kumar et al., 2012; Staib et al., 2020). The auditory cortex receives multiple ascending inputs from subcortical structures involved in emotional processing. Injections of a retrograde tracer in the rostral STG of the macaque monkey showed strong projections to basolateral amygdala, suggesting that this area is polysensory in function (Aggleton et al., 1980; Stefanacci & Amaral, 2000). In addition, work by Aggleton and colleagues showed heavy projections from the superior temporal sulcus to the lateral nucleus of the amygdala in the macaque (Aggleton et al., 1980; Stefanacci & Amaral, 2000). An fMRI study in human volunteers showed that the acoustic features of sounds can modulate the effective connectivity from the auditory cortex to the amygdala, while valence modulates the effective connectivity from the amygdala to the auditory cortex (Kumar et al., 2012). These results suggest a complex interaction between the auditory cortex and amygdala based on the assignment of emotional valence of the acoustic stimuli. The auditory cortex also projects to the prefrontal cortex (Romanski et al., 1999a), indicating it is involved in social cognition (Adolphs, 2009), and that it facilitates the integration of sensory information and higher-order cognitive functions, crucial for processing social cues and auditory information necessary for effective communication (Plakke & Romanski, 2014).

In addition to the modulation of the activity of the STG by emotional stimuli, there is also evidence that the STG is involved in social communication (Kanwal & Rauschecker, 2007; Romanski et al., 1999b). A recent study in gerbils found that the primary auditory cortex is essential for auditory social learning (Paraouty et al., 2023). The authors showed that blocking the auditory cortex impaired social learning and that social exposure improved the sensitivity of the auditory cortex to auditory task cues (Paraouty et al., 2023). Another recent study in the macaque monkey showed that neural activity in the STG is enhanced in response to species-specific vocalisations paired with a matching visual context, or when

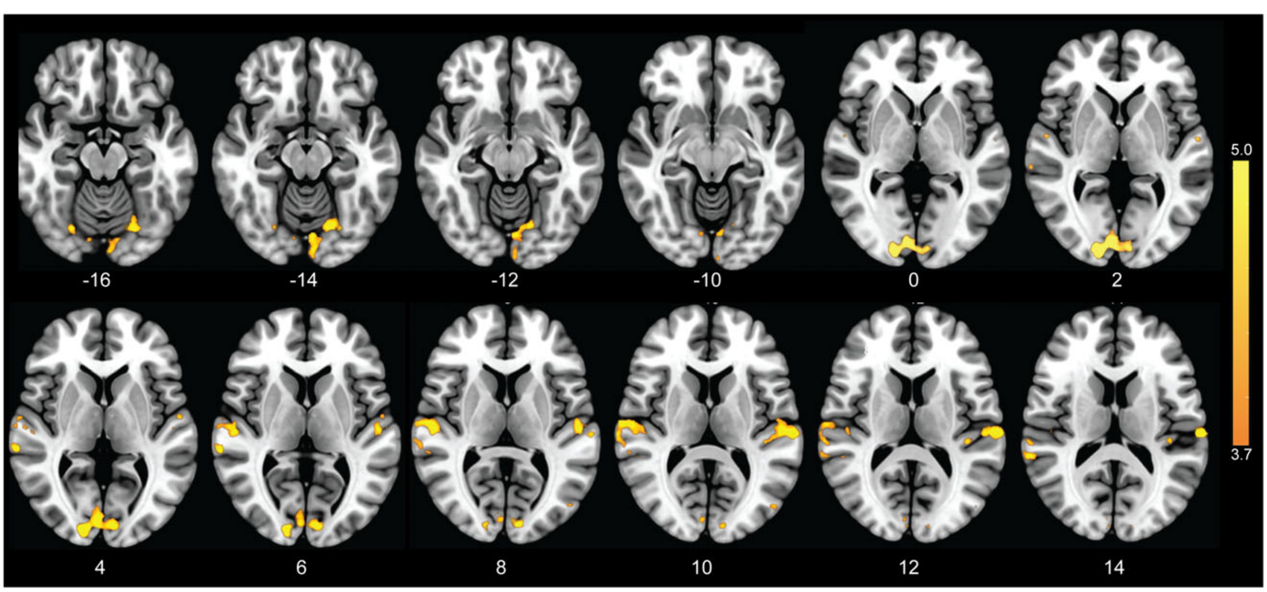

Figure 3. Effects of odor on ISC during negative movie clips (full run). The colorbar represents regions with increased ISC during negative movies (i.e., higher ISC) ($P < 0.05$, FDR-corrected). Right part of the images refers to the left side of the brain. Numbers below the slices refer to z-levels in MNI space. ISC increased in the right calcarine area, bilateral STG, superior occipital gyrus, cerebellum, left MOG, and right fusiform and lingual gyri.

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Table 3. Effects of odorant on ISC during negative movie clips for full run and split run

	Brain structure	Size	Side	MNI Coordinates x	y	z	t-stat
Full run	Calcarine	5148	R	16	−93	2	8.5
	Superior temporal gyrus	1503	R	66	−16	10	6.2
		1291	L	−64	−23	12	7.2
		251	R	64	−39	16	5.6
		210	L	−60	−35	16	4.9
		79	L	−58	−9	2.7	4.8
		34	R	62	−9	4.2	4.4
	Superior occipital gyrus	281	R	26	−91	24	5.6
	Cerebellum	201	R	24	−73	−16	5.4
		103	L	−32	−65	−19	4.8
		32	L	−18	−85	−22	4.2
	Middle occipital gyrus	48	L	−49	−78	10	4.4
Split run	Supramarginal gyrus	710	R	66	−37	26	6.1
		197	L	−64	−39	30	4.7
	Middle temporal gyrus	500	L	−50	−57	6.4	5.5
		118	R	48	−57	10	4.6
	Inferior temporal gyrus	77	L	−56	−47	−14	4.7
	Inferior occipital gyrus	56	L	−26	−95	−8	4.3
	Middle occipital gyrus	52	L	−44	−69	2	4.2
	Superior temporal gyrus	40	L	−54	1	1	4.3
	Lingual gyrus	40	L	−23	−61	−10	4.3
		36	L	−21	−100	−12	4.1

Abbreviations: R = right hemisphere; L = left hemisphere.

vocalisations follow context-congruent visual information (Froesel et al., 2022). Recent fMRI studies in humans confirmed the role of the STG in interpersonal communication. Notably, Parkinson and co-workers showed that synchrony in the STG was highest among close friends and decreased with increasing social distance. Other brain areas where similar results were reported included the inferior and superior parietal cortex, SMG, nucleus accumbens, caudate, putamen and amygdala (Parkinson et al., 2018). The fact that our results showed that adding an odor increase ISC in the STG may therefore suggest that odors make us more similar in how we perceive the surrounding world around us, and that odors stimulate social attraction.

Outside of the STG and middle temporal area, we found that ISC during odor exposure was also increased in the occipital cortex (calcarine and lingual gyrus). This is in line with previous studies showing that together with the auditory areas, visual areas are among the most synchronized during watching audio-visual movies (Gruskin & Patel, 2022; Nummenmaa et al., 2012). The increase in ISC in occipital areas during the odor condition may be driven by connections between olfactory and visual areas. Seminal work by the group of Amaral (Amaral et al., 2003; Freese & Amaral, 2005) showed that there are feed-back projections from the amygdala to all levels of the ventral visual stream. Since the amygdala, together with the piriform cortex, is part of the primary olfactory cortex, this provides a pathway of how olfactory input may modulate sensory processing within different levels of the ventral-stream visual cortical hierarchy.

Our study also clearly shows that the effect of an odor on ISC depends on the emotional valence of the movie clips. Indeed, clearly distinct patterns of increased ISC were found when analyzing the results for the positively and negatively-valenced movies separately. While watching negative emotions during odor exposure, increased ISC was measured in vision-related areas, the calcarine, lingual gyrus and MOG, along with auditory-related regions like the STG (Adolphs, 2013). Earlier studies showed increased ISC in vision-related brain areas during negative emotion-related movie scenes (Hasson et al., 2004; Lahnakoski et al., 2014; Nummenmaa et al., 2012). The lingual gyrus and cuneus support visual attention and the processing of emotionally salient information (Palejwala et al., 2021; Vanni et al., 2001). The MOG integrates visual and social cues, interacting with the prefrontal cortex and amygdala to mediate social responses (Pitcher et al., 2011; Pourtois & Vuilleumier, 2006). The fact that odor increased ISC in the occipital brain areas may be explained by afferent projections from olfactory regions to the occipital cortex (Amaral et al., 2003; Freese & Amaral, 2005). This modulation highlights the potential of odors to influence the

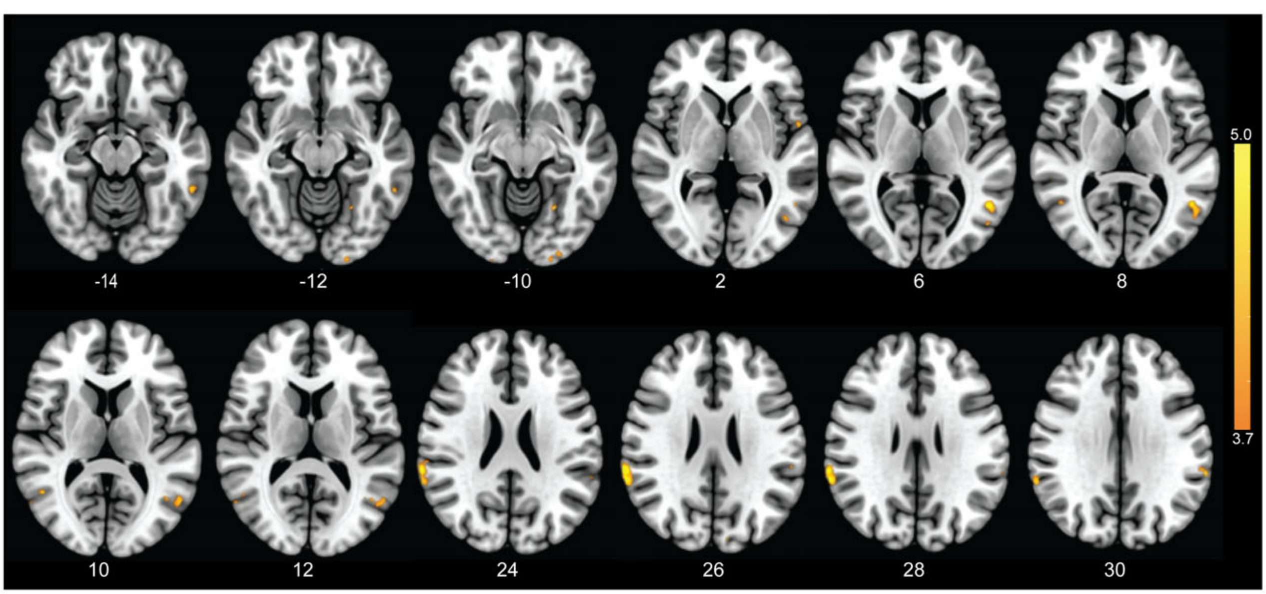

Figure 4. Increased ISC in the second compared to the first negative movie clips during odor exposure (split run technique). Colorbar: increased ISC during negative movies under odor exposure. Numbers below the slices refer to z-levels in MNI space. A large cluster of increased ISC was found in bilateral supramarginal gyrus, with additional clusters in bilateral middle temporal gyrus, left inferior temporal and occipital gyri, left MOG, STG, and lingual gyrus.

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Table 4. Effects of odorant on ISC during positive movie clips for full run and split run

	Brain structure	Size	Side	MNI Coordinates *x*	*y*	*z*	*t-stat*
Full run	Angular gyrus	492	L	−62	−58	36	4.4
		147	L	−40	−65	34	3.6
	Precuneus	210	L	−2	−61	32	3.6
		67	L	−6	−58	44	3.9
		41	R	6	−56	24	3.7
	Cuneus	181	L	−2	−70	24	4.6
	Cerebellum	80	R	10	−75	−28	4.0
		71	L	−26	−73	36	3.8
	Precentral gyrus	76	L	−37	−23	70	3.4
	Posterior cingulate gyrus	62	R	4	−49	32	3.8
	Superior frontal gyrus	45	R	24	59	16	3.3
Split run	Superior parietal gyrus	1012	L	−34	−59	64	4.5
		75	R	20	67	66	3.2
	Inferior temporal gyrus	594	L	−50	−65	6	3.4
		113	R	52	−57	10	2.9
		51	L	−44	−59	4	3.4
	Lingual gyrus	566	L	−22	−99	12	3.6
	Middle temporal gyrus	226	L	−57	−64	4	3.4
	Inferior frontal gyrus	191	L	−48	11	30	4.1

Abbreviations: R = right hemisphere; L = left hemisphere.

processing of negative emotions and social dynamics, enhancing social and group cohesion, and empathy.

Interestingly, the effect of odor on ISC changed over time. The split-run analysis revealed significantly larger effects of the odor on ISC in bilateral SMG, as well as in left STG, MOG, and lingual gyrus during the second of the negatively-valenced movies. This temporal modulation suggests that the integration of olfactory information relies on sustained sensory input and continuous processing, highlighting a complex dynamic where sensory modalities are differentially engaged over time in response to olfactory cues. The progressive enhancement of odor-induced effects over time may result from multiple interacting factors, such as the cumulative sensory and affective impact of prolonged odor exposure, a gradual intensification of emotional resonance, dynamic adjustments in neural synchrony, or a combination thereof. Further research is warranted to systematically disentangle and quantify the relative contributions of these mechanisms.

Our findings suggest that odor modulates neural synchronization in response to both fear and sadness, enhancing the brain's ability to process social and emotional information during negative emotional experiences. Concerning the SMG, this structure plays an important role in social cognition, particularly with respect to empathy, perspective-taking, and emotional regulation. The SMG, especially in the right hemisphere, is involved in affective and cognitive empathy and empathy for pain (Kogler et al., 2020; Lawrence et al., 2006; Narumoto et al., 2001; Thye et al., 2024; Wada et al., 2021). The SMG also plays an important role in theory of mind (Frith & Frith, 2005), allowing people to understand that others may have different thoughts, beliefs and emotions to their own, which is crucial for social interactions as it helps to interpret others' intentions and actions (Schurz et al., 2017; Tholen et al., 2020). Finally, the SMG is crucial to overcome emotional egocentricity bias in social judgments (Silani et al., 2013; Weigand et al., 2021) and processing of social cues (Hooker et al., 2010).

While watching positively-valenced movies under odor exposure, ISC increased in left angular gyrus, precuneus and posterior cingulate cortex, cuneus, precentral and superior frontal gyri, and cerebellum (Frith & Frith, 2012; Zaki & Ochsner, 2012). However, odor did not affect ISC in STG. The precuneus and posterior cingulate cortex are associated with social cognition, self-referential thinking and autobiographical memory (Alcalá-López et al., 2024; Cavanna & Trimble, 2006; Maddock et al., 2003; Zhang et al., 2022). Interestingly, it was shown that patients suffering from anosmia have gray matter reductions in several brain areas, including the precuneus (Lee et al., 2022). The precuneus is involved in self-referential thinking and memory, supporting the recall of positive social interactions and enhancing empathy (Cavanna & Trimble, 2006; Frith & Frith, 2012). The precuneus is activated during empathic and forgivability judgments, highlighting its role in understanding others' intentions and fostering successful social interactions. The precuneus and posterior cingulate cortex are also part of the default mode network (Smallwood et al., 2021). Together, this suggests that the precuneus is key in linking positive emotions and social cognitive processes, promoting empathy and social understanding (Cavanna & Trimble, 2006). As with the negative emotions, we measured a time-dependent effect of odor exposure on the ISC for the positive emotions. Compared to the first movie, ISC increased in parietal and prefrontal areas, the lingual gyrus, and the middle and inferior temporal gyri. The lingual gyrus, known for its role in complex visual processing (e.g., recognizing letters, shapes, and colors), also contributes to the storage and recall of visual memories related to intricate visual scenes. This suggests that odor exposure enhances synchronization in brain regions associated with both visual processing and memory during positive emotional experiences (Davis et al., 2021; Roland & Gulyás, 1995; Taylor et al., 1998).

Finally, our results are in line with the psychological construction theory of emotions (Barrett, 2017). Currently, there are two dominant emotion theories, the basic emotion theory and the psychological construction theory (Gündem et al., 2022). According to the former, emotions are discrete, innate and automatic, and involve specific physiological patterns. In contrast, the psychological construction theory posits that emotions are shaped by individual experience, culture, language, and context. There are no universal, discrete emotion patterns. The brain interprets bodily sensations within a situation and constructs an emotion based on both past experiences and social learning.

Subjective ratings of valence and intensity did not differ between the odor and control condition. This could be explained by the fact that these ratings were done offline, after the subject had left the MRI and without the presence of the odor. Future studies should consider performing the offline valence and arousal ratings in the same conditions (during odor exposure) as during MRI. For the physiological data, no such effect was observed during the movies. This could be due to selective effects on the sympathetic compared to the parasympathetic nervous system. Alternatively, heart rate may be too imprecise to capture the subtle effects of an odor, and future studies might consider measuring heart rate variability instead. Similarly, the lack of a significant effect of odor exposure on respiration rate could be due to respiration frequency being a too crude measure to detect subtle changes.

This study has several limitations that need to be considered when interpreting the results. First, since the movies were played in a fixed order, we cannot rule out specific order effects when assessing the effects of positively and negatively-valenced movies. Next, different movie clips were used in the odor and control conditions. The reason thereto was that each participant was scanned twice, and the use of the same movie clips would entail the risk of emotional contagion or habituation across conditions. We searched for pairs of movie clips which were not only matched for

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valence and arousal, but also for theme, speed of action and content. Nevertheless, we cannot completely rule out the possibility that subtle differences in narrative or visual features may have influenced our results. An alternative approach would have been to use a between-subject design in which participants see the same movie clips but in the two conditions. Other limitations are that we tested for the effect of only one type of odor and that the number of participants was rather limited, even though each participant served as its own control. Future studies are therefore needed to test for the reproducibility of the current findings in a larger sample size (Pajula & Tohka, 2016) and to test whether the here described results can be generalized to other odor categories. These studies could alternatively use EEG (Maffei et al., 2020; Maffei, 2020) or fNIRS, which are more accessible and affordable, better suited for naturalistic settings, and allow for easier implementation of true hyperscanning protocols.

Conclusion

In summary, the present results show that odor exposure enhances synchronicity of brain activity across participants watching emotional movies. Our results further show that the brain areas showing odor-induced alterations in ISC depend on the emotional valence of the movies. Our results add novel insights in the social brain and underscore the complex interaction between olfaction and emotion.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S1355617725101082.

Data availability. Data are available on request to the authors. In that case, the corresponding author should be contacted.

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